What Does Agonistic Dominance Imply in Bonobos?

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Introduction

Hierarchy in Bonobos: An Up-to-date Review

Social dominance is a relevant factor in the study of animal behavior, primatology in particular (Bernstein 1981, Walters and Seyfarth 1987, Newton-Fisher 2004). Social dominance is determined by repeated interactions between pairs of individuals, thus dyadic interactions are important in shaping the nature of the relationship (Hinde 1976). Given that social dominance allows each individual to resolve intragroup contests without engaging in energetically expensive, risky, agonistic interactions, the dominant individual (one with the higher probability of winning any contest) generally acquires the contested resource with only a minimum cost of time and energy, while the subordinate individual (one with the lower probability of winning) avoids wasting both time and energy in a contest that it is likely to lose anyway (Newton-Fisher 2004). Therefore, both individuals avoid potential injuries, which are expected to be greater for the subordinate. This view of dominance is generally based on agonistic interactions and is more precisely defined as agonistic dominance (Bernstein 1981, Walters and Seyfarth 1987, Drews 1993, Mason 1993).

On the other hand, dominance style refers to the pattern of expressed asymmetry in agonistic relationships (de Waal 1989, de Waal and Luttrell 1989): it refers to how dominants treat subordinates and vice versa (de Waal 1996). Many studies have revealed dominance style in chimpanzees (*Pan troglodytes*), in which males are fairly linearly ranked, whereas females generally are not (Wittig and Boesch 2003). Our knowledge of dominance style in *Pan paniscus,* however, is still controversial (Hohmann and Fruth 2003, Paoli et al. 2006a).

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In wild bonobos, dominance ranks have been consistently recorded among males (Furuichi 1997, Furuichi and Ihobe 1994, Kano 1992), but are generally not so clear among females (Kano 1992). In captive bonobos, Franz (1999) and Vervaecke et al. (2000a) described a linear hierarchy with results drawn from both sexes taken together. Specifically, Vervaecke et al. (2000a) showed the occurrence of a linear hierarchy in the bonobo colony of Planckendael (Belgium). Franz (1999) also reported linearity of hierarchy in the Stuttgart and the Wuppertal bonobo groups. De Vries et al. (2006), Stevens et al. (2005b), and Stevens and Vervaecke (this book) showed that the steepness of the bonobo dominance hierarchy fluctuates slightly in different groups. In addition, Stevens and Vervaecke (this book) suggested that in bonobos, dominance relationships between males and between females can be semidespotic. Paoli et al. (2006a) showed that, in a group of unrelated adult bonobos (Apenheul Primate Park, the Netherlands), there was unclear non-linear hierarchy in one study period whereas there was a fairly clear hierarchy in another period, though it just fell to reach statistical linearity. Thus, the dominance style of bonobos may be loose and differentially expressed in diverse groups and/or even in the same group with shifting conditions.

Another peculiarity of bonobos is that they show no formal sign of subordinance, unlike chimpanzees' pant-grunting and bobbing (Kano 1992, Furuich, 1992, Furuichi and Ihobe 1994, Wrangham 1999). In fact, the meaning of pant-grunting in *Pan paniscus* (de Waal 1988, Bermejo and Omedes 1999) remains ambiguous, and in some bonobo groups it is rare (Furuichi and Ihobe 1994, Palagi, 2006). Further, de Waal (1987) and Hohmann and Fruth (2000) hypothesized that genito-genital rubbing signals dominance, but recent data from the Apenheul colony showed no overall asymmetry in performance or invitation to this behavior (Paoli et al. 2006b). Vervaecke et al. (2000a) suggested that even peering (Kano 1992) expresses subordinance, but it is surely not ritualized and appears to be highly polyvalent (Furuichi 1989, Ihobe 1991, Stevens et al. 2005a).

Contrary to the evident male-oriented chimpanzee society, bonobo male bonds are definitely weak (Kano 1992, Parish 1994, White 1996, Fruth et al. 1999, Palagi et al. 2004). In addition, females often dominate males: in fact, even though the adult female is generally slightly physically smaller than the adult male, she is either co-dominant or has a moderate dominance advantage over her male counterpart (Kano 1992, Furuichi 1997, Vervaecke et al.,, 2000a). In agreement with this view, as reported by Vervaecke et al. (2000a), the alpha position in bonobo colonies is often occupied by a female. As stated by Wrangham (1999), the relative lack of interest of male bonobos in high status may be partly a consequence of a system that unites concealed ovulation (Paoli et al. 2006b) with multiple mating, thus reducing the benefits of being a high-ranking male (Kano 1992, Furuichi, 1997, Vervaecke et al. 2000a).

Thus the literature on the dominance style of bonobos is often contradictory and sometimes incomplete. Further research is needed to enhance the understanding of this subject.

Filling the Gap: Additional Investigations

We aim to extend the understanding of the bonobo dominance style. The emerging picture is that *Pan paniscus* shows a flexible and complex society in which agonistic dominance exists, though with variable linearity. Thus, if agonistic dominance occurs in bonobos, what is its meaning? In the attempt to clarify what agonistic dominance implies in bonobos, we focus on some important traits of their social behavior, trying to relate them to the observed rank in two different study periods. We use new data and a review of our published findings to clarify some major aspects about bonobo dominance that have not been adequately described:

1. Linearity and steepness of hierarchy
    - How does linearity vary along with shifting group conditions?
    - How does steepness vary according to changes in linearity of hierarchy and group composition?
2. Individual attributes
    - Does sex influence the dominance rank?
    - Does rank correlate with age and body mass?
3. Social and sexual interactions
    - Does rank correlate with:
    i. Grooming exchange
    ii. Food-sharing exchange
    iii. Peering exchange
    iv. Frequency of genito-genital-rubbing (GG-rubbing) and GG-rubbing invitation exchange
    - Does rank determine any asymmetry in the pattern of performance of GG-rubbing (mounter and mountee roles)?
    - Do males benefit from higher rank in copulatory rate?
    - Post-conflict behavior
    - Does rank influence reconciliation and consolation levels?

Methods: Study Groups, Data Collection and Analysis

We collected behavioral data during two observation sessions (July-October 2000 and April-July 2002) on the group of *Pan paniscus* housed at the Apenheul Primate Park (Apeldoorn, The Netherlands), first established in 1998. The composition of the colony varied over the time (Table 2.1). Details on the study group and the methods used for i) collecting data on agonistic dominance, ii) testing the linearity of hierarchy, and iii) determining the rank using David's scores are described in

Table 2.1 The colony of *Pan paniscus* in the Apenheul Primate Park (Apeldoorn, The Netherlands). Individuals marked with an * died after the first session of observations (July-October 2000). All the bonobos from Democratic Republic of Congo (DRC) were previously housed in a Rescue Center and came from different collection sites

Subject	Sex	Class	Date of Birth	Origin, Arrival Date
H, Hani*	M	Adult	1989, wild	DRC, 1998
MB, Mobikisi	M	Adult	1981, wild	Antwerp,1996
MW, Mwindu	M	Adult	1985, wild	DRC, 1998
J, Jill	F	Adult	1985, captivity	San Diego, 1997
R, Rosie*	F	Adult	1989, wild	DRC, 1998
MO, Molaso	F	Adult	1985, wild	DRC, 1998
Z, Zuani	F	Adult	1990, wild	DRC, 1998
LO, Lomela	F	Adult	1992, captivity	Frankfurt, 1998
LI, Liboso	F	Juvenile	1997, captivity, Zuani's daughter	DRC, 1998
T, Tarishi	M	Infant	1998, captivity, Jill's son	Apenheul
K, Kumbuka	F	Infant	1999, captivity, Molaso's daughter	Apenheul

Paoli et al. (2006a). Tables 2.2 and 2.3 report the frequency of aggressions and displacements for each study period and the calculated rank (David's score).

The steepness of hierarchy is a measure which can vary between 0 (a complete egalitarian, or shallow hierarchy) and 1 (a steep or despotic hierarchy) and is independent from the number of individuals, thus useful for comparing different conditions. It is defined as the absolute slope of the straight line fitted to the normalized David's scores (calculated on the basis of a dyadic dominance index corrected for chance) plotted against the subjects' ranks (de Vries et al. 2006). While the linearity depends on the number of established binary dominance relationships and the degree of transitivity in these relationships (Appleby 1983), the steepness measures the degree to which individuals differ from each other in winning dominance encounters. Linearity and steepness are complementary measures to characterize a dominance hierarchy. To obtain a steepness measure that varies between 0 and 1, it is necessary to convert David's scores into normalized David's scores (NDS) to control for differences in group size, as suggested by de Vries et al. (2006). The use of NDS allows one to obtain steepness values which are independent from the number of individuals characterizing a social group.

We took into account behavioral data collected via scan sampling at 5 minute intervals, and focal animal sampling (Altmann 1974) in both observation periods. We collected data on grooming by scan observations (session 1: 352h, session 2: 356h) whereas we collected data on food-sharing, peering, GG-rubbing and copulations via focal animal sampling (session 1: 41h *per* individual, session 2: 57h *per* individual).

To evaluate the exchange of social interactions we used ratios calculated as logarithm [(performed +1) / (received +1)] per individual, thus obtaining an index that is positive when the individual gives more than it receives and negative when it gives less.

When trying to relate conciliatory and consolatory levels to the observed rank, given that with a break-up approach (considering the two periods separately), post-conflict interactions were insufficient for a proper evaluation, we used the following method:

Table 2.2 Frequency of aggressions and displacements. Observed during 450 hours. Rate/hour = 0.67. Unknown relationships 3.6%, one-way relationships 50%, two-way relationships 46.4%. Weak and non-significant improved index of linearity (Matman, 10,000 permutations): h’ = 0.428, P = 0.252 one-tailed; Directional Consistency Index DC = 0.63

	Recipient									
Actor	JILL	HANI	MOBIKISI	ZUANI	LOMELA	ROSIE	MOLASO	MWINDU	**Total**	**David’s score**
JILL	–	41	22	2	34	5	6	15	125	17.44
HANI	28	–	7	0	8	2	0	25	70	4.79
MOBIKISI	1	1	–	9	6	1	3	12	33	0.05
ZUANI	1	1	1	–	3	1	1	0	8	−2.08
LOMELA	0	4	10	12	–	1	3	6	36	−3.22
ROSIE	0	0	1	0	2	–	1	0	4	−3.51
MOLASO	0	1	0	0	15	0	–	1	17	−3.84
MWINDU	0	0	5	1	1	0	0	–	7	−10.98
Total	30	48	46	24	69	10	14	59	300	

1) We determined NDS as suggested by de Vries et al. (2006).
2) We then calculated the mean value for the NDS between the two periods for each individual (individuals present only in the first period held the value of the first period).
3) We determined the group mean for all individual mean NDS.
4) The animals showing a value of mean NDS over the group mean were high-ranked (J, H, MB); the others were low-ranked (LO, Z, R, MO, MW).
5) We compared the levels of reconciliation (corrected conciliatory tendency, CCT) and consolation (triadic contact tendency, TCT) via the Mann-Whitney test for two independent samples, using CCT and TCT levels published in Palagi et al. (2004). CCTs and TCTs are percentage values.

We used the Spearman test to evaluate the correlation between rank and exchanged social interactions in the whole group and then separately in females in both study periods. Unfortunately, the correlations could not be carried out for males because there were only three adult individuals.

When comparing the GG-rubbing frequency in each dyad with the rank distance, we evaluated the latter via the absolute value of the difference in David's scores between the two individuals of the dyad. We then used MatMan's row-wise correlation tool with 10,000 permutations and a two-tailed test.

Results

Linearity of Hierarchy

During the first period of observations, the matrix of aggressions and displacements (Table 2.2) showed a weak and non-significant linearity index (h' = 0.428, p = 0.252, one-tailed) and a directional consistency index of 0.63. In one dyad (Mwindu-Rosie), no interactions occurred; therefore the percentage of unknown relationships was 3.6%.

During the second period of observations, the matrix (Table 2.3) showed a fairly high linearity index (h' = 0.91) just failing to reach statistical significance (p = 0.055, one-tailed). The directional consistency index was 0.88, but in four dyads no interactions occurred; therefore the percentage of unknown relationships was 26.7%.

Steepness of Hierarchy

In the first study period (Table 2.2), the steepness value is 0.378 (Fig. 2.1a). When we tested the observed steepness against the null hypothesis of random wins for all pairs of individuals (randomization test procedure with 2000 repetitions), we

Table 2.3 Frequency of aggressions and displacements. Observed during 516 hours. Rate/hour = 0.48. Unknown relationships 26.7%, one-way relationships 33.3%, two-way relationships 40%. Almost-significant improved index of linearity (Matman, 10,000 permutations): h' = 0.91, P = 0.055 one-tailed; Directional Consistency Index DC = 0.88

	Recipient							
Actor	MOBIKISI	JILL	MOLASO	LOMELA	ZUANI	MWINDU	**Total**	**David's score**
MOBIKISI	–	10	3	5	2	71	91	6.32
JILL	5	–	2	50	6	69	132	4.48
MOLASO	1	0	–	0	0	0	1	−1.07
LOMELA	1	0	0	–	5	8	14	−1.21
ZUANI	0	5	0	1	–	0	6	−1.75
MWINDU	2	0	0	0	0	–	2	−6.78
Total	9	15	5	56	13	148	246	

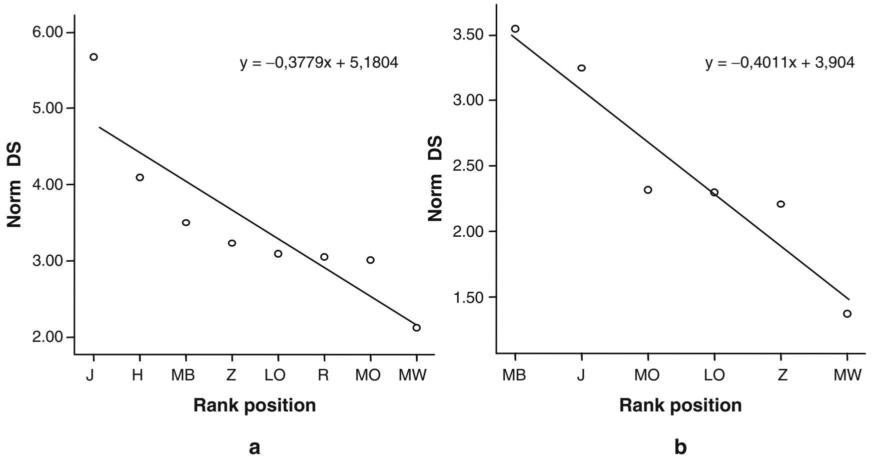

Fig. 2.1 Steepness of hierarchy in the first (a) and the second (b) study periods. Norm DS = Normalized David's scores.

obtained a non-significant value (P = 0.07). That means the hierarchy cannot be defined as steep.

In the second period (Table 2.3), the steepness value is 0.401 (Fig. 2.1b). When we tested the observed steepness against the null hypothesis of random wins for all pairs of individuals (randomization test procedure with 2000 repetitions), we obtained a significant value (P = 0.026), allowing us to label the hierarchy as steep.

Individual Attributes

Rank and Gender

David's scores of males and females obtained from the first study period are not statistically different (Mann-Whitney test: U = 7, $n_1 = 3$, $n_2 = 5$, n.s., two-tailed). The Mann-Whitney test is not applicable to compare David's scores of males and females from the second study period due to small sample size. Nevertheless, the ranks of males and females seem to be comparable in the group.

Rank and Age/body Mass

Individual values of David's score of both sexes taken together are not significantly correlated with age or body mass in either observation period (age, first period: rs = 0.025, n = 8, n.s., two-tailed; second period: rs = 0.58, n = 6, n.s., two-tailed; body mass, first period: rs = 0.307, n = 8, n.s., two-tailed; second period: rs = 0.319, n = 6, n.s., two-tailed; Paoli et al., 2006a). When considering only females, we obtained the same results (age, first period: rs = 0.462, n = 5, n.s., two-tailed; second period: rs = 0.105, n = 4, n.s., two-tailed; body mass, first period: rs = 0.224, n = 5, n.s., two-tailed; second period: rs = 0.211, n = 4, n.s., two-tailed). Thus, individual attributes do not noticeably influence rank.

Social and Sexual Interactions

Exchanged Social Interactions

The grooming ratio is not correlated with rank in either study period (first period $r_s = 0$, n = 8, n.s., two-tailed; second period: $r_s = 0.43$, n = 6, n.s., two-tailed). We obtained the same result for food sharing ratio and rank (first period $r_s = 0.24$, n = 8, n.s., two-tailed; second period: $r_s = -0.6$, n = 6, n.s., two-tailed). Similarly, rank is not correlated with the ratio of peering in either period (first period $r_s = 0.167$, n = 8, n.s., two-tailed; second period: $r_s = -0.086$, n = 6, n.s., two-tailed). Even the ratio of invitation to GG-rubbing is not correlated with rank (first period $r_s = -0.4$, n = 8, n.s., two-tailed; second period: $r_s = 0.2$, n = 6, n.s., two-tailed) and the result is the same for comparisons of the GG-rubbing frequency in each dyad with the observed rank distance (Matman's row-wise correlation, first period: Kr = 13, $tau_{rw} = 0.44$, n.s., two-tailed; second period: Kr = −3, $tau_{rw} = -0.26$, n.s., two-tailed). Accordingly, rank-related asymmetries in social interactions are not apparent in the bonobo group.

Rank and Postural Pattern in GG-rubbing

Paoli et al. (2006b) reported the absence of any overall asymmetry in the pattern of performance of GG-rubbing among all female dyads (mother-daughter pairs excluded, immature individuals included), though in some dyads there was asymmetry. Specifically, even top-ranking females (J and Z, tables 2.2 and 2.3) performed GG-rubbing as mounter or mountee in relation to different partners (J: 433 bouts as mounter, 522 as mountee: Z: 127 as mounter, 272 as mountee).

Copulations and Male Rank

In the first study period, copulations performed by males during focal observations were not equally distributed ($\chi^2 = 29.7$, df = 2, $p < 0.001$), Hani (the alpha male according to David's scores) having the highest frequency (n = 70), followed by Mwindu (n = 34) and Mobikisi (n = 22) (Paoli et al., 2006a). Conversely, in the

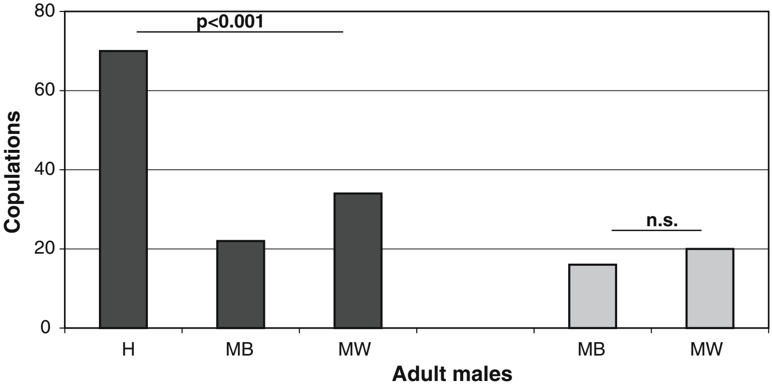

Fig. 2.2 Frequency of male copulations in the first (black bars) and the second (grey bars) study periods.

second study period, copulations performed by the two males are comparable (χ^2 = 0.44, df = 1, n.s.; Mwindu: n = 20; Mobikisi: n = 16) (see Fig. 2.2).

Postconflict Behaviors

We found no clear influence of rank on reconciliation in adults: CCT levels in high-ranking and low-ranking individuals are not statistically different (mean CCT = 14.7% ±12.2% S.E. for high-ranking individuals, CCT = 30.8% ±23.0% S.E. for low-ranking individuals; Mann-Whitney test: U = 5.5, n_1 = 3, n_2 = 5, n.s.), though low-ranking subjects showed a higher mean CCT. Even for consolatory levels among adults, there is no statistical difference between high- and low-ranking individuals (mean TCT = 20.8% ±7.2% S.E. for high-ranking individuals, TCT = 20.5% ±10.8% S.E. for low-ranking individuals; Mann-Whitney test: U = 7, n_1 = 3, n_2 = 5, n.s.) (see Fig. 2.3).

Discussion

Complementing the study by Paoli et al. (2006a) on the hierarchy of the Apenheul bonobos, we expanded the overall analysis based on new results. First, the suggested ill-defined hierarchy characterizing the first study period (Table 2.2) has been confirmed by an insignificant steepness value. Conversely, the almost-significant linearity of the hierarchy characterizing the second study period is accompanied by a significant steepness value. Therefore, this additional investigation at the steepness level confirms that an overall change has occurred in the hierarchy of the Apenheul bonobos across the two periods. The deaths of the two adults (Hani and

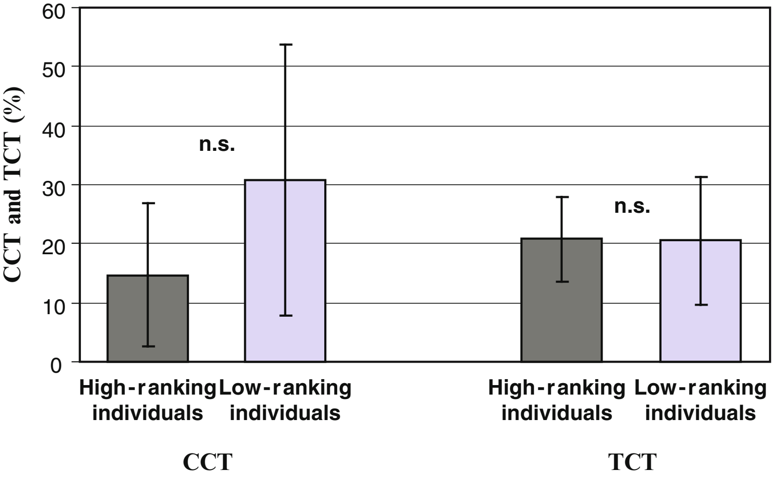

Fig. 2.3 Reconciliation (CCT) and consolation (TCT) levels ± SD in the Apenheul adult bonobos as a function of rank.

Rosie) after the first study session, and the effects of their relationships upon other group members may account for the different results of the two periods. They belonged to the middle/low-ranking class, which according to Furuichi (personal communication), generally shows unclear and non-linear relationships: a decrease in middle/low-ranking individuals reduced the number of uncertain relationships, thereby increasing linearity and steepness in the second study period.

Considering individual attributes, there is no correlation between age and rank in the group or in females during either study period, in contrast to findings by Vervaecke et al. (2000a). Moreover, no correlation between body mass and rank was observed in the group or in females during either study period, which is in line with findings by Vervaecke et al. (2000a). Tests for sexual influences on dominance rank via David's scores of males and females reveal no statistical difference, in both the first and second study periods. Thus, it appears that in Apenheul bonobos, being male or female is not an effective predictor of likely social status.

Considering exchanged social interactions, Vervaecke et al. (2000b) described the occurrence of up-hierarchy grooming in agreement with Seyfarth's model (1980). We used a different approach to assess the occurrence of correlation between rank (David's scores) and grooming exchange. In fact, we correlated individual ranks with the grooming exchange index calculated for each individual, whereas Vervaecke et al. (2000b) employed matrix correlations and an arbitrary assignment of ranks (from high = 6, to low = 1) to the six individuals of the Planckendael colony, thus creating a ranking method which seems less accurate in comparison to David's scores. Given our definition of the exchange index, a ratio of performed over received, a negative correlation between rank and grooming ratios might be expected if subordinate individuals groom more than they are groomed. There is no correlation in either study period. Our results do not agree with those by Vervaecke et al. (2000b), though we underscore that we used a different approach. Another possible explanation for the difference is that the Planckendael bonobos always have been described as strictly linearly ranked (Vervaecke et al. 2000b), whereas the Apenheul bonobos are not. Thus, it may be that the steeper and more linear the hierarchy, the higher the chance to observe a correlation between rank and grooming exchange. However, in our second study period, with an almost-significant linearity of hierarchy and significant steepness, there was no clear correlation, and moreover, the observed tendency (evaluated by the positive Spearman's r_s) suggested a possible, though non-significant, positive correlation (i.e., down-hierarchy grooming) instead of a negative one. Stevens et al. (2005b) also reported the absence of up-hierarchy grooming in the Apenheul colony, which is in line with our findings.

There is no correlation between rank and food-sharing exchange, in either study period, although there are opposite overall tendencies per the sign of r_s. Thus, in the Apenheul bonobo group, high- and low-ranking individuals seem to share and receive food from others to the same extent. The other findings on exchanged social interactions are in line with this framework: there is no correlation between rank and peering exchange, rank and ratio of invitation to GG-rubbing or between GG-rubbing frequency in each dyad and the observed rank distance. All these results indicate a hierarchy-independent distribution of the exchange of social interactions in the Apenheul group.

Further, GG-rubbing, besides not being correlated with rank, showed no asymmetry in the role of performers according to rank (Paoli et al. 2006b). Furuichi (1989) reported similar results, whereas de Waal (1987) and Hohmann and Fruth (2000) described asymmetries in initiation and performance of genital contacts, with high-ranking females more often the mounter (top position) than the mountee. However, the life history of a social group and individual temperaments may influence the patterns of a given behavior to a great extent.

Although we could not test for a correlation between male rank and copulatory frequency (cf. chimpanzees: Newton-Fisher 2004, bonobos: Kano 1996), it is remarkable that copulations were not equally distributed among males in the first study period, with the highest ranking male (Hani) accredited for about 51.5% of the total copulations. Conversely, in the second study period, copulations were equally distributed among males, with the new highest ranking male (Mobikisi) accredited for 44.4% of them. Previous studies on captive and wild populations have indicated various contradictory results. In wild bonobos, Kano (1996) reported a positive relationship between dominance and copulation. Conversely, Gerloff et al. (1999) and Furuichi and Hashimoto (2004) reported the absence of such an effect, illustrating that high-ranking males do not necessarily have the highest copulation rates. Stevens et al. (2001) reported that in some captive groups, males do not monopolize copulations, and even where an unequal distribution of copulations among males occurred, the alpha male did not perform the majority of copulations (Marvan et al. 2006). Our data do not clarify the mixed evidence on the subject.

However, we suggest that the high female rank observed in the Apenheul and other bonobo groups may imply that the correlation between dominance rank and copulatory frequency of males may be disturbed by the mate choice of females (Furuichi 1992, Kano 1996, Fruth et al. 1999), which could be inferred from the long-lasting and frequent maximum swelling characterizing bonobo females (Paoli et al. 2006b). This interpretation is also consistent with the absence of any information on sexual coercion by bonobo males: high-ranking females may choose their mating partners with few or no objections from other males. In addition, the distinctive temperament of each male may play a primary role in determining his attitude to exert monopolization of females, even if the male is a high-ranking individual. For example, in the Apenheul group, Mobikisi was the second-ranking individual in the first study period and the top-ranking one in the second session, but he always showed the lowest copulation frequency.

Another relevant aspect characterizing bonobo sociality is their post-conflict behavior: they reconcile and console to a great extent (de Waal 1987, Palagi et al. 2004). Friendship, evaluated by contact sitting and grooming frequencies, positively affected the level of reconciliation (Palagi et al. 2004), thus supporting the “good relationships hypothesis” (Aureli et al. 1989), and consolation levels were comparable among adult males and females. Our results suggest that bonobo post-conflict behavior is not noticeably affected by rank: high- and low-ranking individuals do not show significantly different rates of reconciliation and consolation. Nevertheless, the mean value of reconciliation in high-ranking individuals is lower than that of low-ranking ones. This finding might be interpreted, even with caution, as the effect of the nature of conflicts among high-ranking animals. In fact, a high-ranking individual is generally the victim of aggression by another high-ranking animal (a higher-ranking individual is more likely to be an aggressor (Tables 2.2 and 2.3). Thus, closely-ranked animals may be more interested in trying to outrank each other than in repairing a relationship put at risk by the aggression between them. In fact, the shifting of the hierarchy is a never-ending process that is probably more evident at the top. In addition, good relationships (Palagi et al. 2004) are more important than rank asymmetries in determining the level of reconciliation. The fact that comparable TCT levels occurred in high- and low-ranking bonobos suggests that social status implies no privilege in receiving reassurance gestures by third-parties. De Waal and Aureli (1996) stated that consolatory affiliations seem to be more common in egalitarian than in despotic societies, i.e., the “social constraints hypothesis.” Egalitarian is not a proper term for bonobos, which should be defined as tolerant. Nevertheless, bonobo society is surely not despotic. Thus it is not surprising to observe high consolatory levels in the species. Our finding of no consolatory asymmetry related to rank fits perfectly into the overall scenario on the dominance style of bonobos: in a condition where the social structure is flexible (Hohmann and Fruth 2002, 2003), tolerant and loose, consolation is probably not offered up in the hierarchy as an appeasement gesture, e.g. to a high-ranking victim, but instead is more likely driven by other complex mechanisms such as empathy.

Conclusions

It is difficult to determine what agonistic dominance implies in bonobos: we did not single out any clear benefit of being a high-ranking individual in terms of asymmetries in social interactions. Even the evidence for a positive relationship between male rank and copulations was mixed when comparing the results of the two study periods and reviewing the literature. Parish (1994, 1996) showed that dominance ranks fit perfectly with feeding priority in a captive group of bonobos: specifically she illustrated that all adult females had priority over the sole adult male. We have no datum on feeding priority from our study group, but the result by Parish seems compatible with data from wild groups, wherein females are rarely attacked by males and enjoy feeding priority (Wrangham 1993, Furuichi 1997, Furuichi and Hashimoto 2002). Even if it is problematic to draw generalizations, we can suggest that a likely primary benefit of being a high-ranking individual is the priority of access to food resources, and that a high social status is generally observed in females, including the Apenheul group. This, along with the availability of large food patches and feed-as-you-go foraging characterizing bonobos (Wrangham 2000), may provide a basis for the occurrence of mixed-sex parties regardless of the female swelling phase (Furuichi 1997, Gerloff et al. 1999). In fact, in this framework where females have high status and feeding priority, their costs for group-living are reduced and their reproductive success is probably increased (Mulavwa et al. this volume).

In addition, an emerging relevant aspect is that bonobos are characterized by a flexible society with constantly shifting relationships in both the wild and captivity (Hohmann and Fruth 2002, Stevens and Vervaecke this book). Yet, given that detailed data on dominance are relatively scarce in wild groups, we strongly encourage further investigations in the field to document more thoroughly the bonobo social system, including ecological data, e.g. changing food availability/quality, in the overall scenario. This may help the understanding of the relationships among social status, feeding priority and reproductive strategies in this species.

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